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Discriminating uniparental and biparental breeding strategies by monitoring nest temperature

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Birds exhibit a wide diversity of breeding strategies. During incubation or chick-rearing, parental care can be either uniparental, by either the male or the female, or biparental. Understanding the selective pressures that drive these different strategies represents an exciting challenge for ecologists. In this context, assigning the type of parental care at the nest (e.g. biparental or uniparental incubation strategy) is often a prerequisite to answering questions in evolutionary ecology. The aim of this study was to produce a standardized method unequivocally to assign an incubation strategy to any Sanderling *Calidris alba* nest found in the field by monitoring nest temperature profiles. Using drops of >3 °C in nest temperature (recorded with thermistors) to distinguish incubation and recess periods, we showed that the number of recesses and the total duration of these recesses from 09:00 to 17:00 h UTC allowed us reliably (99.1% after 24 h and 100% when monitoring the nest for at least 4 days) to assign the incubation strategy at the nest for 21 breeding adults (14 nests). Monitoring nest temperature for at least 24 h is an effective method to assign an incubation strategy without having to re-visit nests, thereby saving time in the field and minimizing both disturbance and related increase in predation risk of clutches. Given the advantages of our method, we suggest that it should be used more widely in studies that aim to document incubation strategies and patterns in regions where ambient temperatures are at least 3 °C below the median nest temperature.

Keywords: arctic, *Calidris alba*, discriminant function, incubation strategy, nest attendance, nest temperature, parental care, shorebirds.

Parental care consists of any parental expense (e.g. in time or energy) that benefits offspring and represents a key component of animal breeding systems (Clutton-Brock 1991). In birds, incubation is one of the most important aspects of successful reproduction (Deeming 2002). At least two main incubation strategies coexist in birds during the incubation period: biparental, when both partners of a pair cooperate to incubate, and uniparental, when only one of the two adults incubates (see Cockburn 2006 for a review). The evolution of these different strategies has been the subject of a great number of studies and hypotheses (e.g.

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Reynolds & Székely 1997, Cockburn 2006). Given the extreme diversity in their breeding systems and incubation rhythms (Reynolds & Székely 1997, Székely *et al.* 2007, Bulla *et al.* 2016), shorebirds, which comprise some 320 species, are an ideal taxon for studying the evolution of breeding strategies. Within this group, the incubation strategy is most often presumed to be fixed within species, but some species can exhibit multiple patterns of care within local populations, ranging from biparental to uniparental incubation by males or females (Webb *et al.* 1999, Blomqvist *et al.* 2001, Reneerkens *et al.* 2011). Unravelling the environmental factors that shape incubation strategies allows for a better understanding of the evolution of avian breeding strategies (Webb *et al.* 1999). For example, both food limitation (Martin 1987, Martin *et al.* 2000) and predation risk (e.g. Fontaine & Martin 2006, Bulla *et al.* 2016) have been proposed as selective pressures to explain incubation strategies.

However, before assessing the possible role of environmental parameters in driving different strategies, one must be able unequivocally to assign the strategy (e.g. biparental or uniparental incubation) of any given nest found in the field. Empirical evidence for biparental incubation is obvious when two adults are seen alternately incubating at a nest. However, when only one adult is recorded (assuming that each adult has the same probability of being recorded during each visit), the probability of documenting a uniparental incubation strategy increases with the number of repeated visits to a nest, but never reaches $P = 1$. For example, $P = 0.94$ after five visits was considered an appropriate observation effort for Sanderling *Calidris alba* by Reneerkens *et al.* (2011). Furthermore, frequent visits to the nest necessarily induce some anthropogenic impacts and can hence bias other parameters under study. Indeed, previous studies showed that the presence of an observer might alter the behaviour of birds (Weidinger 2006, Carey 2011), can reduce nest attendance by parents (Verboven *et al.* 2001), and increase the likelihood of nest abandonment (Götmark 1992) or nest predation (Major 1990). This is particularly the case for studies of species with little or no sexual dimorphism, requiring researchers to catch and mark individually at least one of the incubating adults to identify whether one or two adults are incubating a clutch.

Adults undertaking uniparental and biparental incubation present different behaviours in terms of nest attendance. For example, in order to feed, shorebirds incubating uniparentally have to leave their nests unattended more often than do members of a pair incubating biparentally (e.g. Reneerkens *et al.* 2011, Smith *et al.* 2012). These differences in nest attendance induce differences in temperature profiles in the nest cup, as the temperature immediately drops at the surface of the clutch each time a bird leaves the nest. Temperature data loggers have already been used successfully to study nest attendance by temperature fluctuations in the nest (e.g. Reid *et al.* 1999, Sun *et al.* 2005, Tulp & Schekkerman 2006, Fu *et al.* 2012, Mougeot *et al.* 2014, Bulla *et al.* 2016). As different incubation strategies result in different nest attendance patterns, monitoring nest temperatures should allow us to discriminate between these strategies, provided that the ambient temperature at ground level is sufficiently different (i.e. at least 3 °C lower) from the median nest temperature to allow a clear distinction between incubation and recess periods (the latter here defined as a period when no adult bird is incubating the eggs).

The aim of this study was to produce a standardized method that would unequivocally assign the incubation strategy (uniparental or biparental) to any nest by monitoring temperature profiles in the nest cup. For this purpose, we monitored Sanderling nests with temperature sensors in northeast Greenland. Sanderlings use both biparental and uniparental incubation strategies (Reneerkens *et al.* 2014). We first determined how total recess time and recess frequency differed between the two strategies. We then tested whether the recording was most discriminating during the warmest part of the day (09:00–17:00 h UTC). Finally, we used these differences to produce a mathematical equation that discriminates between the two strategies.

METHODS

Study area and species

The field data for this study were collected from the end of June to early August over three consecutive summers (2011–2013) at Hochstetter Forland (75°10′N, 19°40′W), northeast Greenland. This area has continuous daylight in summer. The vegetation, characterized by prostrate dwarf-shrubs, is typical of the Arctic tundra zone (Walker *et al.* 2005). Mean temperature in July is below 5 °C.

Within this study area, Sanderlings nest at densities reaching a maximum of 10 nests/km² (Gilg *et al.* unpubl. data). Sanderlings are migratory shorebirds that arrive on their Arctic breeding grounds between late May and mid-June (Reneerkens *et al.* 2009). Pairs form quickly after arrival and females lay their eggs in a scrape lined with Arctic Willow *Salix arctica* or Mountain-avens *Dryas* spp. leaves. A complete clutch generally consists of four eggs (one egg laid per day). Incubation normally begins when the third egg is laid. Either one or both parents incubate the clutch for a period of approximately 22 days (Reneerkens *et al.* 2014).

Nest monitoring

Nests were searched by intensively walking in the study area each day during the egg-laying and incubation period. A total of 68 nests was discovered and located over the 3-year study period. Adult birds were caught using small clap nets that were placed over the nest cup. All caught birds were marked with both a numbered metal ring and a unique combination of colour rings (n = 91 birds ringed during the 3 years; an additional 11 adult birds, ringed in 2010, were also observed during the 3 years of this study).

Blood samples (~40 μL per bird) were taken for molecular sexing in sodium heparinized capillary tubes after a careful puncture in the brachial vein with a small needle. The samples were kept in 90% ethanol and DNA was later extracted using the standard phenol-chloroform method. We identified sex using size variation of introns of the Chromo-Helicase-DNA binding protein genes (CHD1-Z and CHD1-W), using 2550F/2718R primer pair (Fridolfsson & Ellegren 1999) and standard PCR and electrophoresis conditions. Intron size variation was easily scored: CHD1-W = 450 base pairs (bp) and CHD1-Z = 750 bp.

The temperature of each nest was monitored using a small thermologger probe (PB-5009-0M6; Gemini Data Loggers, Chichester, UK) connected to a data logger (Tiny Tag TGP-4020; Gemini Data Loggers). The thermologger, which has an accuracy of 0.2 °C at operating temperatures of 0–60 °C and a response time of less than 10 s (www.geminidataloggers.com/fr/probes/thermistor-probes/tinytag-flying-lead-thermistor-probe), was attached at the top of a *c.* 10-cm-long wooden stick and then placed in the middle of the nest cup, at the same height as the upper surface of the eggs, such that it was as close as possible to the brood patch of the incubating adult. The data logger connected with a 60-cm cable to the thermistor was hidden in the ground or vegetation. The data loggers were programmed to register temperature every minute of the incubation period (i.e. the data loggers store a total of 3200 recordings over 22.2 days; an example of 1440 measurements collected over a 24-h period is presented in Fig. 1).

Monitored nests were visited at different times of the day and the total number of visits varied among nests due to logistical constraints. When observers approached a nest, the incubating parent temporarily left the nest. This behaviour allowed us to determine whether the incubating adult had already been captured by observing the presence or absence of colour rings. If not, the bird was captured and ringed. Nests were considered to be incubated biparentally when two different birds were observed incubating the clutch. If the same adult was found incubating during five or more successive visits, the nest was considered (apparently) uniparentally incubated. To support this empirical classification of uniparental nests, we also present (Fig. 2) TinyTag recordings from two nests monitored at the nearby site of Zackenberg for which uniparental incubation was unambiguously confirmed using individual RFID (radiofrequency identification techniques; Reneerkens *et al.* 2011). Once the nest was found empty, the thermistors were removed and the temperature data downloaded using TINYTAG EXPLORER 4.8 software (Gemini Data Loggers).

Data analysis

Of the 68 Sanderling nests recorded, 58 were monitored with thermistors; only 14 of these (seven biparentally incubated and seven presumed uniparentally incubated – five females, one male and one of unknown sex) could be visited five times or more (on five different days or more) before they hatched or were predated. For each of these 14 datasets, we first removed the beginning and the end of the temperature records (i.e. the period before the incubating bird came back after it was ringed and released, and the period following the last recorded temperature drop in the nest, either due to hatching or predation). We then estimated (for complete 24-h period only), the number of recesses (NR; i.e. when the incubating adult leaves the nest and a temperature drop is

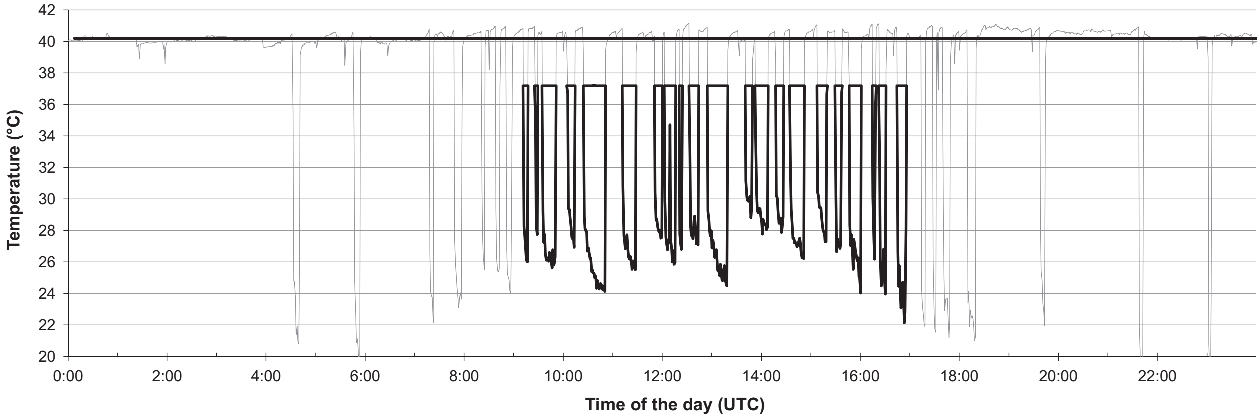

Figure 1. Example of changes in nest temperature (light grey line) over 24 h as recorded with a thermologger probe (PB-5009-0M6) connected to a data logger (Tiny Tag TGP-4020; Gemini Data Loggers, Chichester, UK). The continuous horizontal bold line at 40.175 °C is the daily median temperature of the nest; the other bold lines presented below, between 09:00 and 17:00 h UTC, represent the recesses as defined and used in our method, i.e. periods with nest temperature 3 °C below daily median nest temperature (here 37.125 °C). In this uniparentally incubated nest, a total of 21 recesses could be identified (TDR: 242 min) during the 8-h period used for our discriminant analyse ($D = 3.66$). Note that most recesses occurred during the warmest hours of the day, and the cooling of the nest during the recesses is therefore reduced.

recorded) and the total duration of these recesses per 24-h period (TDR), according to three different threshold values used to distinguish incubation and recess periods. First, we used the same threshold value as Bulla *et al.* (2014), i.e. we considered that a nest was incubated when its temperature was within 3 °C of the median temperature recorded over the 24-h period (and conversely that a recess occurred when the temperature was below this median temperature −3 °C threshold; Fig. 1). We then tested two alternative threshold values: median T°C −1 °C and median T°C −5 °C. Lastly, we estimated NR and TDR using the same three threshold values but only for the 8-h period from 09:00 to 17:00 h UTC, which corresponds to the warmest period of the day when most recesses occur (Reneerkens *et al.* 2011, Smith *et al.* 2012). By doing so, we produced six different combinations of NR and TDR values for each day and each nest, to be used in the models (see below). In Figure 1 and in actograms presented in the Supporting Information, this four-step extraction procedure is presented graphically for the median −3 °C threshold and the 8-h period: the entire time series (thin line) represents the nest temperatures as recorded by the thermistors (first field phase), the upper full lines (covering 24 h) are the calculated median for every full day of record (second phase), and the shorter lines below (green line in Appendix S1) cut the recording between 09:00 and 17:00 h UTC and at 3 °C below the daily median (third phase). The fourth and last phase of the procedure consists of counting the number of occurrences (or NR) and the cumulated duration (TDR) for each monitoring day, of all parts of the time series that are found below the threshold temperature.

Statistical analysis

Using R 3.1.2 software (R Development Core Team 2016), incubation strategies were investigated following a two-step approach. First, we performed linear mixed models (LMMs) using the R package *nlme* to assess the influence of the assigned strategy (uniparental vs. biparental) on both NR and TDR and for each of the six filtering procedures described above. In the LMMs, the assigned strategy was fitted as a fixed effect and nest identity as a random effect. Second, we performed linear discriminant analysis (*lda*) on the six combinations of NR and TDR values (see above) to estimate linear coefficients (i.e. the values of NR or TDR that best discriminate uniparental and biparental nests), using the *lda* function implemented in the *MASS* package of R (Venables & Ripley 2002), with the prior probabilities of class membership set to 0.5. We used a leave-one-out cross-validation method to estimate the proportion of correctly assigned nests by discriminant function

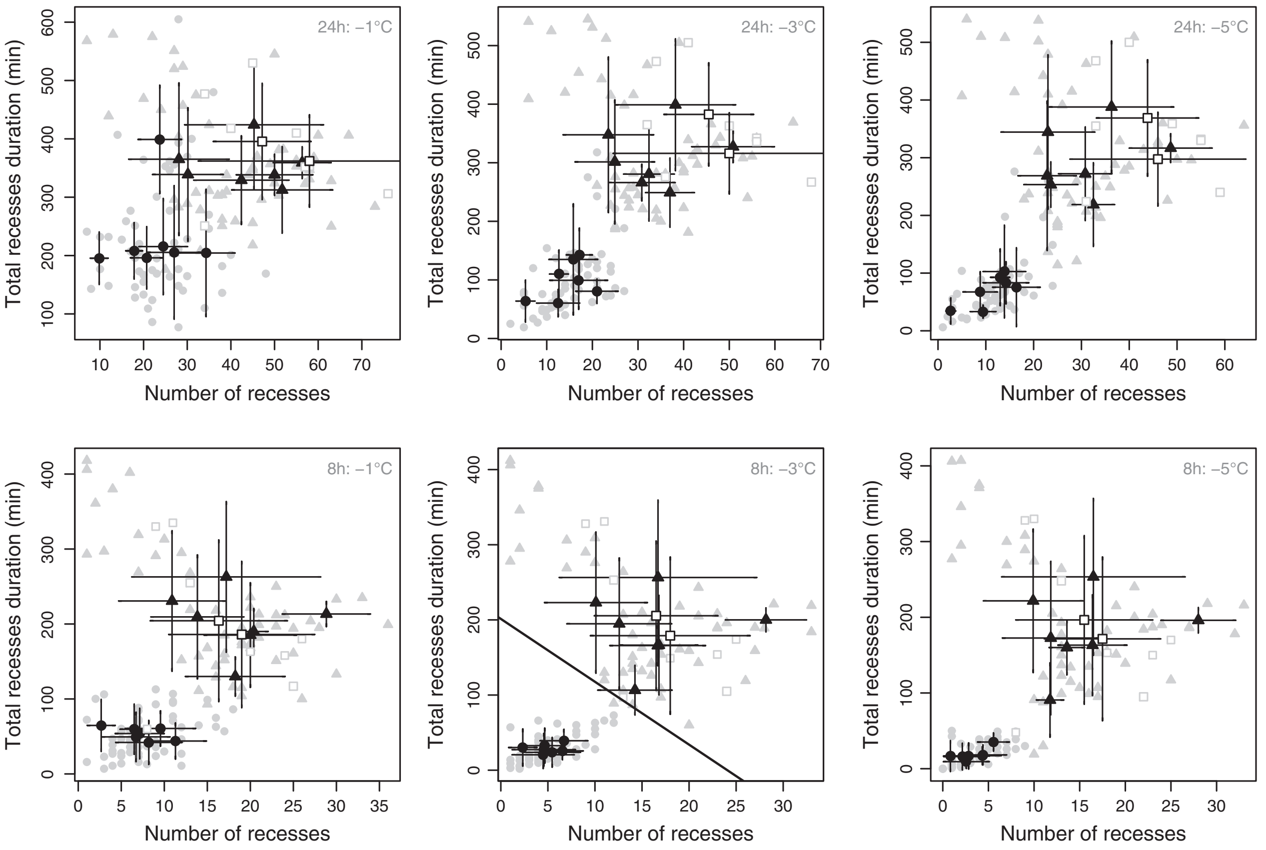

Figure 2. Differences in the nest attendance (number and total duration of recesses) of Sanderlings between incubation strategies, based on our data from seven uniparentally incubated (triangles) and seven biparentally incubated nests (circles); two confirmed uniparentally incubated nests from Reneerkens *et al.* (2011) (open squares) are also included for comparison; see Methods. Upper panels: values recorded over 24-h periods. Lower panels: values recorded during 8-h periods (09:00–17:00 h UTC). From left to right, values estimated with differences to the median nest temperature of −1 °C, −3 °C and −5 °C (see Methods). Grey symbols show the daily estimates. Dark symbols show the means (± sd) of daily estimates for each of the 16 nests. The oblique line on lower central panel shows the discriminant equation (see Results).

analyses. Using this method, the incubation strategy is predicted for each day from the *lda* function obtained after a given nest had been removed from the dataset. We compared the results of the leave-one-out cross-validation tests to identify the temperature threshold (−1 °C, −3 °C or −5 °C), the length of the period (24 or 8 h) and the combination of variables (i.e. the total duration of recesses TDR and/or on the number of recesses NR) that allowed identification of incubation strategy with the best accuracy.

RESULTS

The graphical results obtained for nests (i.e. mean NR and TDR values based on at least five daily recordings; dark symbols in Fig. 2) never overlapped between uniparentally and biparentally incubated nests. This result (100% correct graphical assignment of nests) was independent of the three different threshold values used to define recesses, and of the two distinct periods used to score NR and TDR. Exact values are given in Table 1a for the −3 °C threshold. Between 09:00 and 17:00 h UTC, adults incubating uniparentally left their nest for on average seven times longer and three times more often than biparentally incubating adults (Table 1a). LMMs further confirmed that NR and TDR significantly differed between bi- and uniparental incubators (Table 1b).

The model based on a −3 °C threshold for an 8-h time period (central lower panel on Fig. 2) was the most powerful, with 99.1% of the daily values of NR and TDR (grey symbols in Fig. 2)

Table 1. (a) Descriptive statistics: mean, standard deviation (sd) and 95% confidence intervals (95% CI); numbers in parentheses are means estimated only for days when no visits occurred at the nests (i.e. excluding human-induced recesses). (b) Linear mixed models for total duration of recesses (TDR) expressed in minutes and number of recesses (NR), during 24- or 8-h period (09:00–17:00 H UTC), according to incubation strategy (uniparental, $n = 7$, or biparental, $n = 7$) for all days. The threshold value used here is median temperature −3 °C (see Methods). Biparental incubation strategy was the reference level in all LMMs. TDR data were log-transformed to reach normality for LMMs.

	TDR – 24 h	NR – 24 h	TDR – 8 h	NR – 8 h
(a)				
Biparental strategy				
Mean	99.8 (88.7)	15.3 (14.9)	28.3 (26.2)	5.2 (5.2)
sd	58.6	6.2	18.8	2.9
95% CI	84.9–114.8	13.7–16.9	23.5–33.1	4.5–6.0
Uniparental strategy				
Mean	321.6 (316.3)	32.4 (28.8)	199.7 (192.4)	15.6 (15.2)
sd	103.8	12.5	84.3	8.0
95% CI	293.6–349.5	29.0–35.7	177.0–222.4	13.5–17.8
(b)				
Linear mixed models				
Estimate	1.26	19.16	2.10	11.33
se	0.12	4.00	0.15	2.21
df	12	12	12	12
t	10.22	4.82	13.79	5.12
P	0.001	0.001	0.001	0.001

Table 2. Linear discriminant analysis leave-one-out cross-validation tests, on the total duration of recesses (TDR) and on the number of recesses (NR) during a 24- or 8-h period and a combination of both, with median temperature of −1, −3 and −5 °C thresholds (see Methods).

		Cross-validation (%)		
	Measure	Uniparental	Biparental	Overall
−1 °C	TDR_{24}	75.5	78.2	76.9
	NR_{24}	66.0	85.5	75.9
	TDR_8	84.9	100.0	92.6
	NR_8	75.5	89.1	82.4
	$TDR_{24} + NR_{24}$	84.9	83.6	84.3
	$TDR_8 + NR_8$	96.2	100.0	98.1
−3 °C	TDR_{24}	88.7	93.2	91.1
	NR_{24}	81.1	88.1	84.8
	TDR_8	88.7	100.0	94.6
	NR_8	77.4	94.9	86.6
	$TDR_{24} + NR_{24}$	94.3	93.2	93.8
	$TDR_8 + NR_8$	98.1	100.0	99.1
−5 °C	TDR_{24}	86.5	92.6	89.6
	NR_{24}	86.5	92.6	89.6
	TDR_8	78.8	100.0	89.6
	NR_8	86.5	100.0	93.4
	$TDR_{24} + NR_{24}$	94.2	94.4	94.3
	$TDR_8 + NR_8$	94.2	100.0	97.2

matching model assignments (Table 2). The *lda* performed on daily NR and TDR, i.e. with a threshold of −3 °C and an 8-h period, showed that parental strategies could be assigned correctly for all nests and for all but one (99.1%) of the daily measurements (Table 2). Using the discriminant equation (Equation 1), we could safely assign an incubation strategy for any Sanderling nest in northeast Greenland where nest temperature is monitored between 09:00 and 17:00 h UTC, with biparental incubation strategy indicated when $D < 0$ and uniparental incubation strategy when $D > 0$.

$$D = -3.430 + 0.142NR_8 + 0.017TDR_8 \qquad (1)$$

DISCUSSION

Using a continuous temperature monitoring system and statistical discriminant models, we succeeded in unambiguously determining the incubation strategies (uniparental versus biparental) of a high Arctic breeding shorebird based on differences in nest attendance patterns. Although our method was only developed based on 14 reference nests (with ≥five visits; see Methods), and with the exception of the few misleading situations described below and in Appendix S1, we found no evidence of false assignment of incubation strategy using our method on other nests (several hundred to date) monitored with thermistors on two study sites in Greenland (G.O. unpubl. data).

We described nest attendance with two dependent variables: the number of recesses and the total duration of these recesses, estimated over 24 h or between 09:00 and 17:00 h UTC only. In uniparentally incubated nests, recesses were three times more frequent and the total duration of these recesses seven times longer (09:00–17:00 h UTC, which is the warmest period of the day) compared with biparentally incubated nests (Table 1), meaning that the duration of single recesses is on average more than twice as long in uniparentally incubated nests. We suggest at least two non-exclusive reasons for these differences. First, as birds that are uniparentally incubating maintain higher egg temperatures than those that are biparentally incubating (Reneerkens *et al.* 2011), they are likely to have higher daily energy expenditures and may be expected to feed in longer bouts. Second, birds that are incubating biparentally do not have to feed while they are on nest duty, having sufficient feeding time available when they are off-nest (i.e. nearly 50% of the day, as they share incubation duties equally; Bulla *et al.* 2016). Hence, in biparentally incubated nests, recesses can also indicate rapid shifts between the two incubating adults.

For nests where two different adults were attending, our method always returned a D-value (D being the results of the discriminant Equation 1; biparental incubation strategy when $D < 0$ and uniparental when $D > 0$) corresponding to biparentally incubated nests, whereas we only observed one adult attending when the D-value suggested a uniparentally incubated nest.

Our results are in line with previous empirical observations on the same species (Reneerkens *et al.* 2011). Clearly, the trade-off between incubation and foraging is more severe for birds that are uniparentally incubating because incubation duties cannot be taken over by a partner while foraging (Tulp & Schekkerman 2006). By foraging during frequent bouts and by timing such recesses during the warmer periods of the day (between 09:00 and 17:00 h UTC; Table 1), uniparental incubation both optimizes foraging efficiency and minimizes the drop in egg temperatures (which would increase the energy use of the embryo and negatively affect hatchling phenotype or prolong the incubation period; Webb 1987). Indeed, in our study region, arthropod availability depends on air temperature (mainly for flying arthropods such as Lepidoptera and Diptera) and solar radiation (for surface-dwelling taxa such as spiders), which are highest during this period of the day (Høye & Forchhammer 2008). The fact that recesses were nearly twice as frequent during the warmer parts of the day in uniparentally incubated nests (mean: 1.95 recesses per hour between 09:00 and 17:00 h UTC compared with 1.05 recesses during the rest of the day; Table 1) confirms the results previously reported for Sanderling (Reneerkens *et al.* 2011) and four other shorebird species (Tulp & Schekkerman 2006), indicating that in the Arctic, shorebirds that are uniparentally incubating mainly feed during the warm parts of the day despite the continuous daylight.

Other bird species (e.g. shorebirds Western Sandpiper *Calidris mauri* and Baird's Sandpiper *Calidris bairdi*) also show bimodal incubation strategy (both biparental and uniparental incubation occurring within breeding populations, as with Sanderlings) and our method of monitoring nest temperature with thermistors could be used to discriminate uniparental and biparental incubation. In addition, our method can be used to address questions other than discriminating biparental and uniparental incubation. For example, regardless of the incubation strategy, continuous recording of the nest temperature allows, for some species, documentation of the fate of their nest (i.e. successful if nest temperature steadily declines for *c.* 24 h before the brood leaves the nest-site, or predated if it suddenly drops to ambient temperature within a minute) and its timing, greatly improving the accuracy of our estimates of nest survival probabilities. The nest attendance proxies recorded with thermistors (number and duration of recesses, median nest temperature) can also be compared with other biotic (e.g. life history of breeding adults, abundance or activity of local predators or competitors, food abundance) or abiotic (temperature, hygrometry, wind, rain) parameters to assess their possible impact on incubation patterns, breeding success, etc. Finally, because nest monitoring (e.g. assigning an incubation strategy, documenting recess activity or monitoring the nest survival) can be achieved by visiting the nest-site only once during incubation, the disturbance by observers and possible related biases can be reduced to a minimum. Indeed, frequent visits to nests may reduce nest attendance by parents and increase the risk of nest abandonment or nest predation (Ellison & Cleary 1978, Lenington 1979, Westmoreland & Best 1985, Major 1990, Gotmark 1992, Verboven *et al.* 2001, Weidinger 2006, Carey 2011, but see also Ibañez-Alamo *et al.* 2012). This concern is important in the Arctic where many nests are depredated by Arctic Foxes *Vulpes lagopus* (Reneerkens *et al.* 2016), which have an excellent sense of smell (Kolenosky 1987, Lai *et al.* 2015). With our method, a single visit to the nest is enough to deploy the thermistor and ensure nest monitoring spanning the entire incubation period. The thermistor only needs to be collected after the eggs hatched or were predated (i.e. after the expected hatch date, which can easily be estimated during this single visit by floating two eggs; Hansen *et al.* 2011). Also, using our method, the incubation strategy of a nest can be inferred after only 1–2 days, while this is only possible after at least 5 days with daily visits to each nest. Consequently, the ability to assign an incubation strategy before the nest may be predated is much lower using nest visits.

Although the 14 datasets we used produced consistent results, we can list at least four unusual situations in which values derived from Equation 1 could be misleading (some illustrated in the last actograms reproduced in Appendix S1). First, if the stick holding the temperature probe is too short, or the terrain too soft, the sensor can be pushed down by the weight of the incubating bird and the temperature records would then become chaotic (no clear median temperature, higher sd of the time series) and unsuitable for analysis with our methods. Second, if one of a pair of biparentally incubating birds abandons the nest (i.e. if it dies or deserts), the *D*-value (estimated daily) will become positive, indicating uniparental incubation. Even though this represents a correct interpretation of the actual incubation strategy of changing from biparental to uniparental, this should be considered carefully. Third, due to extreme weather events (e.g. stormy winds, prolonged and heavy rainfall), incubating birds can adjust their behaviour (i.e. nest attendance) to improve the survival of themselves or their eggs. For example, a bird that is uniparentally incubating could stay on its eggs during continuous rain to prevent eggs from cooling (hence its nest attendance would appear similar to the one characteristic for biparentally incubating birds – TDR would decrease and the *D*-value become negative). In fact, our observations tend to support the opposite behaviour, with no impact on the assignment of incubation strategy: birds that are uniparentally incubating leave their nests for longer periods during bad weather events, most likely to meet their increasing energy requirements (Tulp & Schekkerman 2006). Finally, if ground temperature differs less than 3 °C from the daily median nest temperature, our filtering procedure would no longer effectively score NR and TDR. To date, we never observed the latter condition in Greenland and we consider the −3 °C threshold used in our estimation of *D*-values the most appropriate for this type of study. Indeed, as stated above (see also Bulla *et al.* 2016), using the −5 °C threshold we would miss some recesses when ambient temperature is above 30–35 °C. Using the −1 °C threshold would result in scoring false recesses when the recorded incubation temperature is not very stable (i.e. when the probe is not in direct contact with the brood patch) or when brief movements of the incubating adult on the nest are counted as recesses (e.g. the higher values seen on the upper left panel of the Fig. 2 than on the two other upper panels are probably best explained by a combination of these two biases).

The data used in our analyses included both the days without and the days with physical visits of researchers to the nests (44% of the total number of monitoring days; i.e. days with human-induced recesses). Including days with visits increased the mean NR by 3% for uniparentally incubated nests but had no impact on biparentally incubated nests (09:00–17:00 h UTC; Table 1a). There was an increase of 4 and 7%, respectively, in the mean values for TDR, for both uniparentally and biparentally incubated nests. Considering the differences of 292 and 734% that exist, respectively, for NR and TDR between both breeding strategies (see above and Table 1a), and given that our discriminant function returned 100% correct assignments, these slight differences could not harm the predictive value of our discriminant function. Indeed, because our analyses include both types of monitoring days, our results are more robust for future use in the field (i.e. they are applicable in situations both when visits occur and when they do not). Although we decided to use all available monitoring days here, we suggest using the mean values estimated only from days without visits (in parentheses in Table 1a), when presenting mean NR and TDR in a biological perspective (e.g. to compare with results from different species, sites or years).

Our method will now allow us to address exciting new questions about the ecology of breeding strategies. For example, we can now assess whether and how shorebirds adjust their breeding strategy (uniparental vs. biparental incubation in the case of Sanderling) in relation to experienced predation pressure (for changes in nest attendance, see Cervencl *et al.* 2011). This would require monitoring both the ratio of uniparentally and biparentally incubated nests at different levels of predation pressure and the respective survival rate of nests in each strategy.

We recommend that temperature data loggers be used more widely in studies that need to document incubation patterns, especially in precocial ground-nesting species. Our method is particularly effective in the Arctic because the median nest temperature measured by thermistors (*c.* 35–40 °C in our study) will always be much higher than the ambient temperature. In 2011, when most nests were monitored, thermistors placed at ground level and exposed to direct sunlight, i.e. in the same environment as unattended nests, recorded maximum daily temperatures between 15 and 25 °C during the Sanderling breeding season. The efficiency of our method in regions where ambient temperature is closer to the incubation temperature, but where nests are often built in shadow, remains to be tested.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Actograms of the 16 Sanderling nests used in this study are reproduced in the Supporting Information file. In this file, we first present the seven biparental nests from Hochstetter Forland, then the seven uniparental nests from the same site and from Zackenberg. Finally, we present a few atypical examples of actograms illustrating possible problems which can arise when interpreting actograms and *D*-values calculated from our Equation 1.